An Investigation on the Anatomical Structure and Relationships of the Labyrinth in the Reptile, the Bird, and the Mammal.

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[Plates 19 and 20.]

The object of this paper is to give a description of the labyrinth of certain animals, illustrating the organ when it is viewed as a whole in examples chosen from the reptiles, birds and mammals.

The method of preparation employed was that devised by the writer and described in the "Labyrinth of Animals," vol. 1, p. 8. By the use of this method new facts have been brought to light, and these enable us to elucidate certain relationships in the anatomical structures which have hitherto been obscure and which anatomists are not agreed upon. The structures referred to are, the aqueduct of the perilymph, the perilymph recess and the round window. A special portion of the paper, therefore, has been directed to this aspect of the subject.

Before proceeding to describe the organs mentioned, the writer would like to thank very cordially those who have assisted him in obtaining material. Since some of the animals are rare and difficult to obtain, it will naturally be understood that the writer is very grateful to those who have given them to him for preparation, and he is glad to have this opportunity of thanking the Zoological Society of London, the Royal College of Surgeons of London, and the Hon. N. Charles Rothschild.

The Membranous Labyrinth of the Monitor (Varanus salvator).

(Plate 19, figs. 1, 2, and 3.)

In extracting the labyrinth of this reptile it was found possible to make a more complete preparation of the organ than was done in any of the reptiles examined hitherto. This has brought into light some interesting facts which help to elucidate considerably the relationship of the reptilian to the avian and mammalian labyrinths.

The organ measures 8 mm. in its greatest length from the junction of the superior and posterior canals to the tip of the cochlea. The *cochlea* measures 3·5 mm. in length from the oval window to the tip, and the tube of the cochlea measured at its base is 1·75 mm. in diameter. The reason why this

measurement of the length of the cochlea appears to be so great relatively to the same measurement in the bird is owing to the fact that, in the reptile, the oval window is situated in the vestibule, while in the bird it is placed some little distance along the tube of the cochlea.

The *vestibule* measures 3·75 mm. in its greatest diameter, and the major axis of the oval window is nearly 1·5 mm. in length.

The *superior canal* measures 4·5 mm. in internal, and 6·5 mm. in external diameter. The greatest distance of the canal from the vestibule is 1·5 mm., and the diameter of the canal itself is 1 mm. The *posterior canal* has internal and external diameters of 4 mm. and 6 mm. respectively. The greatest distance of the canal from the vestibule is 0·5 mm., and the diameter of the canal itself is 0·75 mm.

The *horizontal canal* measures 3 mm. in internal, and 5 mm. in external diameter. The greatest distance of the canal from the vestibule is 1 mm., and the diameter of the tube of the canal itself is 0·75 mm.

In its general shape the labyrinth of the monitor resembles those of other reptiles; that is to say, it is roughly pyramidal. The canals do not present such a constantly curved outline as do those of the bird and the mammal, and in this respect also they are more like those of other reptiles. The perilymph space is well marked in the canals. The horizontal canal, *h.*, has no communication with the posterior canal, *p.*, at the point at which they cross, the monitor resembling the gecko in this respect and differing from all the other reptiles examined by the writer. There is no bridge connecting the upper surface of the saccule with the middle of the superior canal in the monitor, such as was found in the teguixin and the West African python.*

The vestibule in the monitor is very similar to that found in other reptiles, and needs but little remark. The saccule forms by far the larger portion of the vestibule. It is roughly cone-shaped, with the apex of the cone near the junction of the superior and posterior canals. It contains, and is almost entirely filled by, the large otolith mass, *o.s.*, which consists in this, as in other reptiles, of a collection of innumerable minute crystals held together by a semi-gelatinous envelope. The saccule is external to the utricle. The last-named cavity is very small, and is really only large enough to receive the openings of the three canals.

The oval window, *f.o.*, is situated at the lower and posterior portion of the saccule. It is oval in shape, resembling that of the mammals rather than that of other reptiles and birds. It is, indeed, a narrower ellipse than is found in the case of some mammals, such as the echidna and the

* Gray, *op. cit.*, vol. 2, pp. 214 and 222.

kangaroo. It is interesting to note that the oval window is situated further back relative to the saccule and the cochlea than in birds or mammals. Its posterior margin is almost in contact with the ampulla of the posterior canal.

The cochlea, *c.*, is slightly constricted after leaving the lower and inner portion of the saccule, and in the neck formed by this constriction lies the aqueduct of the perilymph, *d.p.* Passing downwards and inwards, the cochlea first bulges slightly and then tapers gradually to end as a cone. It is interesting to notice that, at the tip, the cochlea ends with a little nipple-shaped projection, exactly similar to that found in some of the ratite birds, such as the emu, ostrich and rhea.

The cartilaginous framework within the cochlea which supports the basilar membrane and the lagena, *l.*, is in the form of a long ellipse, the major axis of which is, of course, parallel with the long axis of the cochlea. It does not appear to be rotated upon itself to any very noticeable extent, the two limbs of the framework remaining anterior and posterior respectively throughout their whole course. In this respect the shape of the framework differs from that of birds; but it is similar in another respect to that of at least most birds in that, at its vestibular end, the cartilage bends sharply upon itself.

The ductus perilymphaticus, or aqueduct of the perilymph, *d.p.*, may be demonstrated very clearly in the labyrinth of the monitor, and shows very interesting relationships. It arises on the outer surface of the labyrinth at the junction of the cochlea with the saccule as a fairly wide tube. From this point it curves forward, then inwards, and finally backwards, being in contact with and encircling the neck of the cochlea, and reaches the inner posterior portion of that neck. The ductus perilymphaticus was traced by Retzius* to this point in an allied species (*Psammosaurus caspicus*), but he was unable to trace it further. Its further course is interesting, especially in view of the fact that it throws considerable light upon the relationship of the round window and perilymph recess to the cochlea as found in birds and mammals. After reaching the inner posterior surface of the cochlea, the aqueduct of the perilymph turns slightly downwards, and immediately widens out into a large cavity, roughly heart-shaped, and termed the perilymph recess, recessus perilymphaticus, or recessus scalæ tympani, *r.p.*

The perilymph recess has roughly five surfaces. The first of these surfaces is the uppermost, and is small, consisting merely of an opening *o.p.*, by means of which the perilymph recess communicates directly with the arachnoid space, and it therefore permits of free interchange between the cerebro-spinal fluid and the perilymph. The inner wall passes from above and within

* Retzius, 'Das Gehörorgan d. Wirbelthiere,' vol. 2, p. 98.

downwards and slightly outwards. It is roughly rectangular in shape, and its long anterior margin runs close to the tip of the cochlea. This surface is covered entirely by bone. The posterior wall runs from the posterior edge of the inner wall outwards and backwards. The anterior outer wall runs from the anterior edge of the inner surface backwards and outwards to meet the posterior wall below the ampulla of the posterior semicircular canal. Lastly the inferior anterior wall, which may be termed the floor of the cavity, looks downwards, forwards and outwards (in fig. 2 the organ is rotated a little clockwise, so that the floor looks downwards, whereas in reality it looks a little forwards and outwards as well). The floor is roughly oval or rectangular in shape, and is entirely uncovered by bone. It is, however, closed by a thin membrane, *f.r.*, and looks directly into the tympanum. This corresponds anatomically, and perhaps also functionally, to the round window of birds and mammals. But this portion of the subject will be referred to later in the paper.

Pigment is found in the labyrinth of the monitor, scattered in specks over the surface of the perilymph recess, including the membrane closing the round window. It is also found over the surface of the cochlea, and more particularly over the walls of the aqueduct of the perilymph. A few specks are found on the wall of the saccule which is adjacent to the cochlea. The distribution of pigment, therefore, is very similar in arrangement to that found in the lizard and teguixin. It is, perhaps, still more interesting to note that the distribution of pigment in the labyrinth of birds in those rare cases in which it is found, the ostrich, rhea and tinamou, is similar to that found in the teguixin, the lizard and the monitor. In the tortoise and the python it is either entirely absent or nearly so, whereas in the gecko it is found equally abundant over the whole surface of the labyrinth.

In addition to the large otolith mass already described as being found in the saccule, there is a string of small otoliths in the cochlea which runs along the basilar portion of the organ, and on reaching the lagenar portion the string of otoliths widens out into a spoon-shaped arrangement along the anterior wall.

Yet another otolith, *o.u.*, is found in the labyrinth of the monitor, and this one is of special interest since it forshadows in the reptile the otolith which is found in the bird. It is seen in that portion of the utricle which runs forwards to the ampullæ of the horizontal and superior canals, and lies internal to, and behind these ampullæ respectively. It is, therefore, in exactly the same position in which the otolith or otoliths (for there are sometimes two) are found in the utricle of the bird. But in yet another respect this otolith is similar to those found in the same position in birds. It consists

of one comparatively large crystal and not of a collection of minute granules as does the large otolith in the saccule.

The Membranous Labyrinth of the Emu (Dromæus novæ-hollandiæ).

(Figs. 4 and 5.)

The labyrinth of the emu is, as might be expected, a large one, larger indeed, than that of any bird that has been examined, except the ostrich.

It measures 17·5 mm. in its greatest length from the uppermost point on the superior canal to the tip of the cochlea. The *cochlea* measures 4 mm. from the anterior margin of the oval window to the tip of the organ. The diameter of the tube of the cochlea immediately in front of the oval window is rather more than 2·5 mm.

The longest diameter of the *vestibule* is 4 mm. and the length of the major axis of the oval window is 2 mm.

The *superior canal* measures rather more than 8·5 mm. in internal, and 11·5 mm. in external diameter. The height of the vertex of the canal above the vestibule is 9·5 mm. and the diameter of the canal at the vertex is 1·25 mm. The *posterior canal* measures 5 mm. in internal, and 7·5 mm. in external diameter. The height of the vertex of the canal above the vestibule is 4·5 mm., and the diameter of the tube of the canal itself is 1·25 mm. The *horizontal canal* has internal and external diameters of 5 mm. and 7·5 mm. respectively. The height of the vertex of the canal above the vestibule is rather more than 3·5 mm. and the diameter of the tube of the canal itself at the vertex is 1·25 mm.

The labyrinth of the emu presents considerable similarity to those of the other ratite birds which have been examined by the writer, viz., the ostrich, the rhea and the apteryx. The similarity is much more pronounced between the emu, ostrich and rhea, than between any of these and the apteryx.

The semicircular canals in the emu are well curved, there being none of the angularity which is found to a certain extent in the apteryx alone among birds. The superior, *s.*, is the largest of the three canals and is of the "drooping" type. The perilymph space is well marked in all the canals and the cristæ acusticæ of the ampullæ are "simple" in character. There is no approximation to a channel of communication between the horizontal and superior canals such as is found in some of the carinate birds. In these respects the labyrinth of the emu agrees with those of the other ratite birds.

In the labyrinth of the emu, as in those of the ostrich and apteryx, there is no communication between the posterior, *p.*, and horizontal canals, *h.*, at the point at which they cross one another. This arrangement is different

from that found in the rhea and in all the carinate birds hitherto examined, with the exception to be described in this paper, the penguin. The significance of this communication has already been discussed, from the evolutionary point of view,* but a few words may, with advantage, be added now. The channel is present in many reptiles, but not in all, *e.g.*, the gecko and monitor. In birds it was supposed to be invariably present until its absence was demonstrated by the writer in the ostrich and apteryx. In mammals, on the other hand, it has only been found to be present in a limited number of the polyprotodont marsupials and the insectivora. In such amphibia as have been examined, the frog and the toad, the channel was found to be present.

It is thus difficult to account for the facts as they are manifest in birds. In their origin from reptiles, birds may either have possessed this channel and it has been lost in the ratite branch, with the exception of the rhea; or they may not have derived it from the reptilian stock, it having been acquired by the carinate birds and by the rhea among the ratitæ. On these two views, suggested by himself, the writer formerly declined to express an opinion as to which was the more probably correct.† But, with the disposition of the canals in the emu, he is now rather inclined to the view that the channel of communication referred to has been acquired by the birds, and is not a remnant of reptilian ancestry. It is, of course, quite impossible to dogmatise, but in view of the fact that in the ostrich, emu, and apteryx, the channel is absent, and that that these are undoubtedly birds of an ancient type, the opinion above expressed seems the more probable, in spite of the fact that the rhea possesses the communication under discussion. Further, in support of this opinion, it should be pointed out that the communication is present in all carinate birds that have been examined by the writer, with the single exception of the penguin; and it is of considerable significance that the penguin is admittedly an archaic type of bird.‡ The writer has in course of preparation the labyrinth of the cassowary, and its examination will throw fresh light upon this point.

As regards the physiological significance of this channel of communication, if there is any such significance at all, it must be admitted that its function is obscure. The channel, when present, only allows of the passage of the perilymph from one canal to the other, the endolymph spaces of the two canals always remaining quite separate.

The cochlea, *c.*, of the emu is, in general, similar to those of the ratite birds.

* Gray, *op. cit.*, vol. 2, p. 95.
† *Op. cit.*, vol. 2, p. 93.
‡ 'Cambridge Nat. Hist.,' vol. 9, p. 94.

That is to say, it is short, and the tube is wide in proportion to its length. The lagena, *l.*, is large, and at the tip the cochlea ends in a little nipple-shaped projection which is peculiarly characteristic of the labyrinth of the ostrich and rhea. The tegmentum vasculosum, *t.v.*, that curious plexus of parallel venous spaces, is found in the emu, as it has been in all other birds hitherto examined, with the single exception of the ostrich. According to Retzius, it is found in at least some reptiles, and the present writer has found it in the apteryx. Its apparent absence in the ostrich is, therefore, most remarkable, and it may be that it is present in a modified form, though the writer was unable to find even a trace of it in three different specimens of the Masai ostrich. In the emu, as stated above, the tegmentum vasculosum is clearly marked, and has an appearance similar to that found in the rhea, but the parallel venous spaces are fewer in number, and rather wider apart than in the latter.

The recessus perilymphaticus, *r.p.*, that large cavity which opens out of the scala tympani of the cochlea, is well developed in the emu as in the other ratite birds. It is, however, more oval in shape than in the ostrich and rhea, in which it bears some resemblance to a sack with corners. On the lower and anterior surface of the perilymph recess is the round window, which is oval in shape, as in other birds and in reptiles. In the emu, the round window is of considerable size, larger, for example, than the oval window, *f.o.* At the opposite end, that is, at the upper posterior portion of the perilymph recess, is the aqueductus perilymphaticus, *d.p.* The latter leaves the perilymph recess directly and, after a short course of 1 or 2 mm., opens into the cranial cavity. Its disposition, therefore, is like that found in the ostrich, the rhea, the common fowl, the tinamou, and some other birds. In the crow, the night-heron, and many of the carinate birds, the aqueductus perilymphaticus opens out of the posterior wall of the perilymph recess, and instead of passing directly towards the cranial cavity, it curves upward in contact with the posterior wall of the perilymph recess for about 2 mm., and then opens into the cranial cavity.

Pigment is not found in the labyrinth of the emu, at least in sufficient amount to be seen by the eye, even when the organ is magnified to ten times its natural size. In this respect, therefore, it differs from those of the ostrich, the rhea and the tinamou.

Otoliths of considerable size are found in the emu; they occupy similar positions as do those in birds generally, and are similar to them in shape. In the vestibule there are two of these crystals, *o.*, and they lie in the utricle immediately behind, and internal to, the openings of the superior and horizontal ampullæ into that cavity. They are flattened from above

downwards. The remaining otolith is found in the lagena, *h.*, and is, as is common in birds, saddle-shaped, with the concave surface facing downwards. Thus the otoliths of the emu are very similar in position and shape to those found in the rhea.

The Membranous Labyrinth of the Rhea (Rhea Americana).

(Plate 20, fig. 6.)

As the labyrinth of the rhea has already been described, there is no need to give a general description of it here. But for the sake of comparison a representation of a portion of the organ is shown.

It will be noticed that the otoliths, both in the vestibule and in the lagena, *o.* and *l.*, are very similar to those of the emu. The cochlea is more bulbous at the inner portion than is that of the emu, but the nipple-shaped termination of the organ is present, though it has been broken in the course of preparation; the place where it has been broken off is clearly seen.

The perilymph recess, *r.p.*, is large in the rhea, and is sack-shaped as in the ostrich, rather than oval as in the emu. The round window, *f.r.*, is shown at the lower, outer, and anterior portion of the perilymph recess; it is large and has the form of a long ellipse.

Pigment is present in the form of minute granules, and is fairly abundant in amount, thus giving a speckled appearance to the perilymph recess. It is almost entirely confined to the perilymph recess, the distribution being similar to that found in the tinamou, whereas in the ostrich pigment is found over the surface of the perilymph recess and also over the adjacent surface of the cochlea.

The Membranous Labyrinth of the Penguin (Spheniscus demersus).

(Figs. 7, 8, and 9.)

The labyrinth of the penguin is large, measuring 16·5 mm. from the vertex of the superior canal to the tip of the cochlea. The *cochlea* measures 4·5 mm. from the anterior margin of the oval window to the tip, and the tube of the cochlea is 2 mm. in diameter at the level of the oval window.

The *vestibule* measures 4 mm. in its greatest diameter, and the major axis of the oval window is 1·75 mm. in length.

The *superior canal* measures 7 mm. in internal, and 10·5 mm. in external diameter. The height of the vertex of the canal above the vestibule is 7·5 mm., and the diameter of the tube of the canal at the vertex is rather less than 1·5 mm. The *posterior canal* measures 4·5 mm. in internal, and 7 mm. in external diameter. The height of the vertex of the canal above

the vestibule is rather less than 3·5 mm., and the diameter of the canal itself at its vertex is rather less than 1·5 mm. The *horizontal canal* has internal and external diameters of 5 and 7 mm. respectively. The height of the vertex of the canal above the vestibule is rather more than 3·5 mm., and the diameter of the canal itself at its vertex is 1·5 mm.

In the specimen of the labyrinth of the penguin which is represented in fig. 7, etc., air-bubbles unfortunately made their appearance in the celloidin in which the structures are embedded, and this interferes to a certain extent with the view of the parts. In addition to this the perilymph recess has been in part broken off.

In its general appearance the labyrinth of the penguin approaches most nearly to that of the red-throated diver among all the birds which have so far been examined. This is particularly noticeable in the cochlea, which terminates not as a rounded or bulbous extremity as in other birds, but comes rather to a tapering point. In both birds the superior canal, *s.*, is of the "drooping" type, and has the form of a long ellipse.

In the canals of the penguin, as in almost all birds, the perilymph space is well marked. The cristæ acusticæ in the ampullæ are "simple," there being only one crest in that portion of the neuro-epithelium which lies on the floor of the ampullæ. There is one peculiarity about the canals of the penguin which should be noted. There appears to be no channel of communication between the perilymph spaces of the horizontal and posterior canals at the point at which they cross, *x*. On close examination there does seem to be contact between the walls of the canals, but no actual channel from one to the other can be found in the specimen from which this description is taken. In this respect, therefore, the labyrinth of the penguin is somewhat similar to those of the ostrich, the emu, and the apteryx, and differs from all other birds which have been examined hitherto.

The cochlea, *c.*, of the penguin is of a rather primitive type in comparison with those of other carinate birds. The organ is proportionately somewhat short, the basilar portion being particularly small in extent.

The cartilaginous structures, *c.f.*, in the cochlea of the penguin deserve notice. It has been stated by some anatomists, that in the avian cochlea there are two cartilaginous plates which unite at their distal extremities in the region of the lagena, while each plate has its own termination at the vestibular end of the cochlea. This statement may be, and probably is, true in respect to some birds, but, as was pointed out by the writer, it is not true of all,* *e.g.*, the rhea. In this bird, the cartilaginous structure consists of

* *Op. cit.*, vol. 2, p. 122.

one piece, which is bent sharply on itself at its vestibular end, while at the distal extremity, in the region of the lagena, the two approach one another and become fused into one. The ellipse formed by the two limbs of the cartilage is, of course, occupied by the basilar membrane. Furthermore, this elliptical cartilaginous framework is curved and also rotated upon itself to a certain extent, so that its concavity looks backward and upwards, the structure being therefore parallel with the curvature of the cochlea itself.

In the penguin there is found almost exactly the same disposition of the cartilaginous framework as that just described in the rhea. That is to say, it does not consist of two plates of cartilage with different points of origin at the vestibular end of the cochlea, but of a single piece in the form of a long ellipse. At the vestibular and middle portions of the cochlea one of the limbs of the ellipse runs along the lower surface of the cochlea and separates the oval window from the large opening which gives access to the perilymph recess. The other limb runs along the upper surface of the cochlea, and through its substance pass those fibres of the cochlear nerve which are destined to supply the basilar membrane. Towards the lagena, however, the cartilaginous framework becomes rotated to a certain extent upon its long axis, so that the lower limb becomes posterior and the upper limb becomes anterior; the two limbs then become fused at the lagena.

This disposition of the cartilaginous framework within the cochlea of some birds is not difficult of explanation when it is remembered that in the reptiles the basilar macula is supported by a single circular or oval cartilaginous ring. The only change in the disposition of the cartilaginous framework which has taken place in the transition from the reptile to the bird is, that the circular ring has been drawn out into a rather long ellipse. Further, a certain amount of rotation round its own long axis appears to have occurred. Thus it comes about that in the proximal portion of the organ the limbs of the cartilage are superior and inferior, while at the lagenar end they are posterior and anterior.

The disposition of the cartilaginous framework in the cochlea of the bird is well seen in the photograph of the Cape gannet, and is undoubtedly the arrangement found in many other birds.*

With respect to otoliths in the labyrinth of the penguin, no conclusions can be drawn from the specimen obtained by the writer. It had lain for several years in spirit, and it is quite possible that the calcareous otoliths had been dissolved by some chemical agent produced during the long immersion in that fluid.

Pigment appears to be entirely absent from the labyrinth of the penguin;

* Gray, *op. cit.*, vol. 2, p. 134.

or, if present, the quantity must be so small in amount that it is invisible to the eye even when the organ is magnified to five or six times its natural size.

It is not possible to give here a satisfactory description of the perilymph recess and round window in the penguin, since in the specimen obtained by the writer the lower portion of the cavity was broken off, carrying with it the round window, if that opening exists in this bird. The destruction of the lower portion of the perilymph recess, however, has had one advantage: it shows clearly the large oval opening, *o.o.*, between that cavity and the scala tympani of the cochlea.

On the upper surface of the perilymph recess in the labyrinth of the penguin there is an opening, *d.p.*, in the wall of the cavity. This dehiscence is oval in shape and occupies the position of the aqueductus perilymphaticus (or aqueduct of the cochlea as it is sometimes termed) in other birds, such as the ostrich, emu, tinamou, etc. It corresponds exactly to the opening which is found in the same position in the monitor, and permits of intermingling of the perilymph with the cerebro-spinal fluid. In other words, the penguin does not possess an aqueductus perilymphaticus in the proper sense of the term, the channel being represented merely by an oval opening.

The Membranous Labyrinth of Echidna aculeata.

(Fig. 10.)

The labyrinth of the spiny ant-eater possesses the special interest which attaches to all the organs of the monotremes. Before going on to consider the relationships of the different parts, however, the measurements may be given.

The organ measures 11 mm. in its greatest length from the outermost point on the posterior canal to the innermost point on the cochlea. The whole diameter of the half whorl of which the *cochlea* consists is 6 mm. and the diameter of the tube of the cochlea itself just before its junction with the vestibule is 1·75 mm. The *vestibule* measures 3·5 mm. in its longest diameter and the major axis of the oval window 1 mm. in length.

The *superior canal* measures rather less than 4·5 mm. in internal, and 6 mm. in external diameter. The height of the vertex of the canal above the vestibule is 3·5 mm. and the diameter of the canal itself at the vertex is 0·75 mm. The *posterior canal* measures rather more than 2·5 mm. in internal, and 4 mm. in external diameter. The height of the vertex of the canal above the vestibule is 3 mm. and the diameter of the canal itself at the vertex is 0·75 mm. The *horizontal canal* measures 2·75 mm. in internal, and 4 mm. in external diameter. The height of the vertex of the canal above

the vestibule is 2·5 mm. and the diameter of the canal itself at the vertex is 0·75 mm.

The cochlea is only possessed of half a turn and the straight distance from the anterior margin of the round window to the tip of the cochlea is 4·5 mm.

As stated above, there are numerous points of interest connected with the labyrinth of the echidna, some of which have been known previously, while others are now recorded. Further, certain errors, which inevitably arise from the attempt to reconstruct a whole larger structure from numerous fine microscopic sections, may be corrected when the organ is viewed as a whole.

Considered as a whole, the labyrinth of the echidna, while approaching rather more nearly the mammalian than the reptilian type, presents several remarkable similarities to the latter. Thus, as has been shown by previous anatomists, there is a lagena, *l.*, at the tip of the cochlea, and this structure is seen in fig. 10 as an oval cavity in that portion of the tip of the organ which lies nearest to the vestibule. It is supplied by a nerve, but it is not possible to say whether otoliths are present in the lagena or not. The specimen lay in rectified spirit for very many years, and it is quite possible that during that time they were dissolved if ever present. Since the processes for ordinary microscopic examination permit the contact of acids, otoliths, when present, are at once dissolved, so that the work of previous anatomists does not elucidate the matter. The question could be decided by preparing a comparatively fresh specimen by the writer's method, by which means otoliths are preserved, as is shown in the case of the reptile and the bird.

It has been shown by previous anatomists that the cochlea of the echidna only possesses a portion of a turn, but, judging from the figures drawn to represent the organ, a somewhat erroneous impression has been conveyed. As a matter of fact, the cochlea, *c.*, of the echidna presents the appearance of a larger portion of a circle than is usually depicted, most representations making it appear very similar to that of the platypus. In reality, the labyrinth of the echidna presents in this, as in other respects, a very considerable advance upon that of the platypus, in which there is only the slightest degree of curvature in the cochlea, with a bulbous knob on the tip of the organ.*

The aqueduct of the cochlea in echidna is a structure whose relationships are clearly reminiscent of its reptilian ancestry. Out of the base of the cochlea there opens, by a large oval aperture, an egg-shaped cavity, which

* Gray, *op. cit.*, vol. 2, p. 81.

corresponds to the perilymph recess of the reptile and the bird, and may be allowed to retain that name, *r.p.* On the outer surface of this perilymph recess is the round window, *f.r.*, and, as if further to express its reptilian character, the round window is markedly oval in shape. The long axis of the round window lies in the horizontal plane, as is the case in the reptile and the bird, and the membrane which closes the window looks directly into the tympanic cavity as in other animals.

On passing towards the cranial cavity the perilymph recess becomes narrowed to form the aqueduct of the cochlea, *p.a.*, which, in its further course towards the cranial cavity, lies above the jugular vein.

The vestibule in the echidna is also similar to that of the reptile except in the matter of size. The saccule forms the larger division of the vestibule, and in this animal, as in all mammals and reptiles that have been examined, the oval window abuts upon the saccule, the utricle being above and behind the latter. In the echidna the oval window, *f.o.*, is almost completely circular in shape, in this respect agreeing with that of the bird and many reptiles, and differing from that of the mammalia, though in certain of the marsupials there is a tendency towards the circular shape. In the echidna, therefore, as also in some reptiles and in birds, the oval window is round, and the round window is oval.

There is yet another primitive feature in the labyrinth of the echidna which has hitherto escaped recognition. That is the existence of a very definite recessus utriculi. In the echidna the recessus utriculi, *r.u.*, consists of a conical diverticulum from the utricle just where the ampulla of the horizontal canal opens into the utricle. The blunt and roughly cone-shaped recessus utriculi passes horizontally backwards and ends in a nipple-like projection just external to the middle of the outer wall of the utricle.

So far as the writer is aware, the presence of a recessus utriculi has not been suspected in any of the mammalia and certainly it has not been found in any of the mammals described by him. In the reptile and amphibian it does exist, but does not always form a prominence on the outer surface of the labyrinth, since the surrounding cavity of the perilymph rounds it off. In some birds, however, it forms a prominence in exactly the same position as in the echidna, and both in the latter and in the bird its floor is supplied by a nerve.*

The extent to which otoliths are present in the labyrinth of the echidna cannot be decided from the specimen in the writer's possession, for the reason above stated, viz., the very long period over which the preparation remained in spirit before the organ was extracted. In fig. 10 there certainly appear

* *Op. cit.*, vol. 2, p. 188.

to be deposits like otoliths immediately internal to the oval window, but the fact that these are otoliths cannot be definitely stated. For reasons above given the ordinary examination of the organ by microscopic sections cannot throw any light upon the matter.

In one respect, however, the vestibule of the echidna's labyrinth is distinctly more like that of mammals than that of at least the majority of reptiles. Its size, relative to the rest of the organ, is small, whereas in reptiles the vestibule is frequently the bulkiest portion of the whole labyrinth and occupies almost all the space contained by the planes of the three canals.

The semicircular canals of the echidna are very definitely mammalian in type (fig. 10, *s.h.p.*). They have entirely lost that angularity which is so characteristic of those of the reptile and of which vestiges are found in the platypus and the sloth.† Further, the junction of the superior and posterior canals is exactly similar to that found in mammals, with the exception of the platypus and sloth. In these two animals, as also in the reptiles, the two canals meet one another abruptly to form the common crus, whereas in the echidna and in mammals generally they approach one another with a gradual curve, so that when they unite a forked disposition of the union is produced.

The perilymph space in the canals is fairly well marked in the echidna, a feature which is invariable in the reptiles hitherto examined, but rather the exception in the mammals. The evolutionary significance of the perilymph space in the canals has already been discussed.‡ It was suggested that the original condition in mammalia presented the appearance of a perilymph space of considerable dimensions, as large, for example, as the endolymph space. In the very great majority of mammals, however, this space in the canals has been very nearly obliterated, but is still present in the primates, including man, in some of the marine carnivora, and in the edentates. Its existence in the echidna lends support to the view that originally the mammalian stock retained this space, inherited from their reptilian ancestor. The space is always present in birds, so far as present investigations have shown. In all animals which possess the space, it is almost entirely confined to the concave portion of the canal.

The white deposits seen in the canals in fig. 10 may be calcareous in character, but they can hardly be considered true otoliths, since, placed as they are at the vertices of the canals, they could have no physiological function similar to true otoliths; for there is no nerve supply to any portion of the canals except the ampullæ. The deposits seen in fig. 10 may be the

* Gray, *op. cit.*, vol. 2, p. 81, and vol. 1, p. 159.

† Gray, *op. cit.*, vol. 1, p. 24.

result of the long sojourn of the head in alcohol before it was given to the writer for preparation of the labyrinths; and the deposits seen in the cochlea and vestibule may possibly be explained in the same way.

In comparing the labyrinth of the echidna with that of the platypus, it must first be noticed that there are greater differences than has hitherto been supposed. The considerable increase in the curvature of the cochlea of the echidna, as compared with that of the platypus, has already been mentioned, and need not be referred to further. But in the canals also the disposition of the structures is very different in the two animals. As was shown above, the canals of the echidna are curved in outline and completely mammalian in type. In the platypus, on the other hand, the superior canal is noticeably angular and it meets the posterior canal abruptly, both of which features are characteristic of the reptilian labyrinth. The specimen of the labyrinth of the platypus obtained by the writer was a poor one, owing to the presence of hæmorrhagic opacities, and it cannot be determined whether that labyrinth possesses a recessus utriculi or not. The aqueduct of the cochlea also was removed in the labyrinth of the platypus, so in this feature also, comparison cannot be made between the labyrinths of the two animals. But in every other feature, at any rate so far as macroscopic evidence goes, the labyrinth of the echidna, though possessing many distinctive reptilian features, is clearly a more definite advance towards the mammalian type than is that of the platypus.

The Relationships of the Aqueduct of the Perilymph, the Perilymph Recess, and the Round Window to one another, and to the Cochlea.

In the labyrinths of the animals just described, certain facts are elicited which throw considerable light upon the difficult question of the relationship of the structures mentioned above. It is still a matter of doubt, in spite of the careful investigations of Hasse, Retzius, Harrison, Gaupp, Versluys and others, as to what particular structure, for example, in birds and reptiles corresponds to the round window of the mammals. The difficulty has, of course, arisen from the fact that investigations have hitherto been made by means of the examination of numerous serial microscopic sections or by casts of the organ, and it is not surprising, therefore, that differences of opinion exist in regard to the relationships of the different structures. By the method employed in making the preparations from which the descriptions in these pages are taken, some at least of the causes of error are eliminated.

In general it may be said, in respect to the relationships of the aqueduct of the perilymph, the perilymph recess, the round window and the cochlea, that in the reptile the condition is the most complicated, in the bird rather

less so, and in the mammal it is comparatively simple. Further, the writer ventures to think that if the structures are viewed as a whole, the process by which this simplification has taken place may be traced in its various stages.

In the monitor the aqueduct of the perilymph opens out of the outer surface labyrinth at the point where the cochlea leaves the saccule. It curves first forwards then inwards and then backwards, thus encircling the neck of the cochlea. It then passes a little backwards and downwards and dilates into the large perilymph recess as described above. The anterior wall of the perilymph recess at its upper and outer part lies in contact with the posterior wall of the cochlea. In the bird there is no sign of the aqueduct of the perilymph surrounding the neck of the cochlea; all the portion of the aqueduct from its commencement to its dilatation into the perilymph recess appears to have become obliterated. But, as though to compensate for this, the adjacent walls of the cochlea and perilymph recess have become fused and an opening appears in this wall by which the perilymph fluid passes direct from the scala tympani into the perilymph recess. This is the condition found in the bird and it is also found in some reptiles such as the alligator.* The perilymph recess remains in other respects similar to that of the reptile. That is to say, it has the large round window (which is really oval both in the bird and reptile) at its lower, outer and anterior portion, and on its upper and inner extremity there opens a very short channel which corresponds to the dehiscence which occupies the same place in the monitor and through which the perilymph in the recess mingles with the cerebro-spinal fluid. Indeed, among the birds examined by the writer this structure still retained its reptilian form in the case of the penguin.

The confusion which has arisen as to what structure in the reptile and bird really represents the round window of mammals has undoubtedly arisen on account of the presence of the opening between the wall of the cochlea and the perilymph recess. Since it has hitherto been supposed that mammals do not possess a perilymph recess, it was naturally assumed that the opening from the cochlea into that cavity corresponded with the round window of the mammals. Now this opening occupies pretty accurately the position of the round window in mammals, but in reality it cannot be said to represent the round window of the bird and reptile at all. As stated above, the round window of these latter lies at the lower and anterior portion of the perilymph recess and looks directly into the tympanum. The round window of the reptile ultimately comes in mammals to occupy the position of the opening from the cochlea into the perilymph recess, and the process

* Retzius, *op. cit.*, vol. 2, p. 121.

by which it does so is illustrated by a transition stage which may be seen in the case of the echidna, and which has hitherto escaped recognition. Though it has not hitherto been suspected, the echidna possesses a definite perilymph recess which communicates with the scala tympani of the cochlea by an oval opening corresponding exactly to that which exists in the same position in birds and in some reptiles, *e.g.*, the alligator. The perilymph recess of the echidna is not so large as in the bird or reptile, and the neck which unites it to the cochlea is not relatively quite so constricted as in these divisions of the vertebrata. Its reduction in size is owing to the fact that it has become a shallower pouch, the sides of the sack having become gathered up as it were. Thus the sack assumes the shape, roughly speaking, of an egg with its long axis horizontal, and that portion of the aqueduct of the perilymph which unites the perilymph recess with the cranial cavity in birds and reptiles tapers off from the posterior end of the perilymph recess in the echidna. Further, this portion of the aqueduct becomes a much longer tube owing to the deposition of bone round about it.

By the same process the round window, which in reptiles and birds occupies only the lower portion of the outer wall of the perilymph recess, becomes raised up in the echidna and occupies the whole breadth of the outer wall of that cavity. It is interesting to note, moreover, that the round window in the echidna still retains the oval shape as seen in the reptile and the bird. Further, by the same process of raising of the round window, the anterior margin of the latter comes almost into contact with the wall of the cochlea at the outer margin of the oval opening between the cochlea and the perilymph recess.

The next step is seen in the kangaroo and wallaby. The oval opening between the scala tympani of the cochlea and the perilymph recess has become much wider, so much so indeed, that the floor of the cochlea sweeps gradually round to join the walls of the perilymph recess. Thus the latter cavity now forms a cone-shaped bulging on the floor of the scala tympani, there being little or no distinction as to the line at which the cochlea ends and the perilymph recess begins. The cone-shaped bulging, which is all that is now left of the latter cavity, has, of course, its base in the cochlea wall, while its apex tapers off into the aqueduct of the perilymph, passing inwards and backwards to open into the cranial cavity.*

By this process of the merging of the perilymph recess into the floor of the scala tympani, it is clear that the round window may be said now to open into the scala tympani, for the bulging on the floor of the latter is now all that is left of the perilymph recess.

* Gray, *op. cit.*, vol. 2, p. 55.

The next stage need only be mentioned, for it consists merely in the reduction of the sharp cone-shaped bulging to a slight round bulging, and is found in many mammals, such as the carnivora and ungulates.*

The last stage is that found in the primates, including man. In it the bulging on the floor of the scala tympani has quite disappeared, its walls having been gathered in, as it were, until they are flush with the rest of the floor of the scala tympani. With this gathering-in process the round window must of necessity come to occupy a position in the outer wall of the scala tympani, and similarly the aqueduct of the perilymph comes to open out quite abruptly from the floor of the scala tympani. In the primates, the aqueduct of the cochlea is almost capillary in calibre throughout the earlier part of its course.†

When the labyrinths of reptiles, birds, and mammals are investigated in this way, it is not difficult to see why misconceptions should have arisen as to which structures in one division correspond with the structures in the other divisions. Thus, what is known as the ductus perilymphaticus in the reptile does not exist in the bird and mammal so far as present investigations show, and, conversely, the ductus perilymphaticus of mammals and birds is represented merely by an oval dehiscence in the roof of the perilymph recess of reptiles.

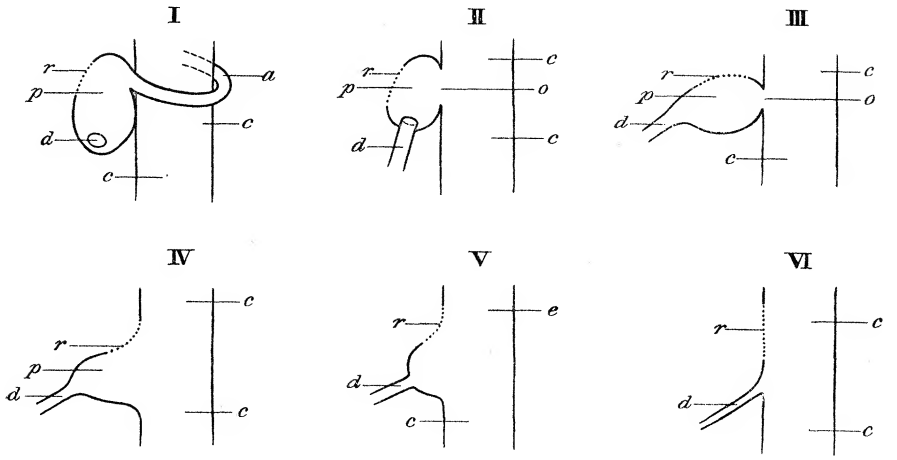
Again, the round window of man and the primates, with most other mammals, corresponds really to two structures in echidna, birds and reptiles, these two structures having come to coincide in the primates, etc. From the point of view of evolution the round window of man and most mammals corresponds with the opening low down in the perilymph recess of birds and reptiles, which is closed by a membrane. But as regards its position relative to the cochlea, the round window of man and mammals corresponds with the oval opening which exists between the cochlea and the perilymph recess of the echidna, the birds, and some reptiles.

Further, by tracing the labyrinth through its changes in reptiles, birds, and mammals by the means of investigation employed, the process by which the ductus perilymphaticus comes to open out of the cochlea is made clear. For it is to be noted that this aqueduct is found in the amphibians before the cochlea has made any appearance as a separate cavity, it being represented only by the macula basilaris. In this division, of course, the ductus perilymphaticus opens out of the vestibule.

It is somewhat difficult to describe these changes in words, and a series of diagrams has therefore been drawn up to show the matter more clearly.

* Gray, *op. cit.*, vol. 1, pp. 91, 137, etc.

† Gray, *op. cit.*, vol. 1, p. 33.



Scheme of the Arrangement of the Ductus Perilymphaticus, etc., in Reptiles, Birds, and Mammals.

Fig. I.—Reptile, Monitor.—*a.*, aqueduct of perilymph. *c.c.*, cochlea. *p.*, perilymph recess. *d.*, dehiscence on roof of perilymph recess through which the perilymph is in direct communication with the cerebro-spinal fluid. This dehiscence becomes drawn out into the form of a short tube in the bird and a long tube in the mammal, and in these two divisions is termed the aqueduct of the perilymph. *r.*, round window, closed by a membrane, represented by a dotted line.

Fig. II.—Bird, Rhea, etc.—*o.*, oval opening between scala tympani of cochlea and perilymph recess ; it is not closed by a membrane. The other letters correspond with those in fig. 1, but it is to be noted that the oval opening, *d.*, in the reptile becomes the tube, *d.*, in the bird. The oval opening, *o.*, is present in all birds hitherto examined and in at least some reptiles, *e.g.*, alligator.

Fig. III.—Echidna.—The letters correspond with those of figs. I, II, etc.

Fig. IV.—Marsupial, Kangaroo.—The letters correspond with those of the other figures.

Fig. V.—Ungulates, Carnivora, etc.—The letters correspond with those of the other figures.

Fig. VI.—Primates, including Man.—The letters correspond with those of the other figures.

DESCRIPTION OF PLATES.

Plate 19, Fig. 1.

The Left Membranous Labyrinth of the Monitor, *Varanus salvator*, viewed from the outer aspect. × 5. The organ is rotated slightly counter-clockwise. The superior canal, *s.*, is to the left ; the posterior, *p.*, to the right ; and the horizontal, *h.*, is seen between them. The horizontal canal has no communication with the posterior canal at the point at which they cross. The large oval saccule is seen filling to a great extent the space between the canals, and the otolith apparatus, *o.s.*, occupies a large portion of the saccule. The single crystalline otolith of the utricle, *o.u.*, is seen internal to and behind the ampullæ of the horizontal and superior canals respectively. The oval window, *f.o.*, is seen opening into the lower posterior portion of the saccule below the arch of the horizontal canal. Immediately to the left of the oval

window the aqueduct of the perilymph, *d.p.*, is seen opening out of the labyrinth at the junction of the saccule and cochlea, and passing round in front of the cochlea, then disappearing behind the inner wall of the latter, and finally reappearing at its posterior border to dilate into the large perilymph recess, *r.p.*, which lies to the right of the cochlea in the plate. The oval surface at the lower and outer portion of the perilymph recess is the round window, *f.r.*, and it will be noticed that it, in common with the other walls of the perilymph recess, is speckled with pigment. Pigment is also seen over the aqueduct of the perilymph and, more scantily, over the lower portion of the saccule and over the anterior wall of the cochlea, *c.*

PLATE 19, FIG. 2.

The Left Membranous Labyrinth of the Monitor, *Varanus salvator*, viewed from the inner aspect and a little below. × 8. The ampulla of the posterior canal, *a.p.*, is to the left, and it will be noticed that the crista acustica is "complex," that is, it has three crests, as is also the case in many birds. The aqueduct of the perilymph, *d.p.*, is seen running backwards over the inner surface of the neck of the cochlea, and then dilating into the large perilymph recess, *r.p.*, the anterior wall of which is in contact with the posterior wall of the cochlea, *c.* The cochlea is seen containing the oval cartilaginous framework and the otoliths, as described in the text. The little nipple-shaped termination to the cochlea is shown, and is similar to that found in most of the ratite birds.

l., lagena.
f.r., fenestra rotunda.
g., inferior angle of posterior canal.
a.p., ampulla of posterior canal.
p., superior angle of posterior canal.
o.s., otolith of saccule.
s., superior canal.
o.u., otolith of utricle.

PLATE 19, FIG. 3.

The Left Membranous Labyrinth of the Monitor, *Varanus salvator*, viewed from the inner aspect and slightly in front. × 8. Taken by reflected light. The oval opening, *o.p.*, on the upper surface of the perilymph recess, *r.p.*, is shown. It is by means of this opening that the perilymph communicates with the cerebro-spinal fluid. The opening corresponds to the aqueduct of the perilymph of birds and mammals. The other parts have already been described in figs. 1 and 2.

p., posterior canal.
s., superior canal.
o.s., otolith of saccule.
a.p., ampulla of posterior canal.
d.p., ductus perilymphaticus.
c., cochlea.
r.p., recessus perilymphaticus.
o.p., opening on upper surface of perilymph recess.

PLATE 19, FIG. 4.

The Right Membranous Labyrinth of the Emu, *Dromæus novæ-hollandiæ*. × 5 *ca.* The organ is viewed from the outer aspect and in front, and is rotated clockwise to the extent of about 20°. The superior canal, *s.*, is of the "drooping" type. There is no communication between the arches of the horizontal, *h.*, and posterior canals, *p.* The cristæ acusticæ in the ampullæ are "simple." The footplate of the columella has been left in position in the oval window, *f.o.* The large egg-shaped

perilymph recess, *r.p.*, is seen behind the cochlea, *c.* The round window is barely visible. On looking through the perilymph recess to its upper and inner wall the narrow opening of the aqueduct of the perilymph, *d.p.*, is seen. The black patches on the walls of the perilymph recess are due to hæmorrhages. No pigment is visible. The nipple-shaped termination to the cochlea is seen below the lagena, *l.*

a.p., ampulla of posterior canal.

PLATE 19, FIG. 5.

Portion of the Right Membranous Labyrinth of the Emu, *Dromæus novæ-hollandiæ.* × 10½ *ca.* Taken by transmitted light and viewed from the outer aspect. One of the otoliths of the utricle is seen as a sharply defined black structure, *o.*, at the top right-hand corner. The parallel venous spaces of the tegmentum vasculosum, *t.v.*, are well shown. The helicotrema, *h.c.*, is seen as an oval opening about three-quarters of the way along the cochlea, *c.*, to the right, with a large vein passing through it. A saddle-shaped otolith is present in the lagena, *l.* The disc-shaped footplate of the columella is seen in its natural position in the oval window, *f.o.*, and it is to be noted that the latter is situated in the cochlea some little distance from its beginning, and is in this respect different from those of the reptiles and mammals. The perilymph recess, the round window, and aqueduct of the perilymph are seen as described in Plate 4, but are more highly magnified.

PLATE 20, FIG. 6.

Portion of the Right Membranous Labyrinth of the Rhea, *Rhea americana.* × 12. Taken by transmitted light and viewed from in front and slightly below. The cristæ acusticæ in the ampullæ are "simple." The otolith of the utricle, *o.*, is seen as a sharply defined black mass internal to and behind the ampullæ of the superior and horizontal canals, and is very similar to the same structure as found in the emu. In the cochlea the tegmentum vasculosum, *t.v.*, is shown and it will be noticed that the parallel venous channels are closer together and more numerous than in the emu. The columella has been removed from the oval window and the latter is more elliptical in shape than is the case in the emu. The large perilymph recess, *r.p.*, is not so definitely oval as in the emu, but is very similar to the perilymph recess in the monitor. The round window, *f.r.*, is large, occupying the whole of the floor of the perilymph recess: it is elliptical in outline and the membrane which closes it is richly pigmented. The walls of the perilymph recess are also pigmented. A saddle-shaped otolith is seen in the lagena, *l.* The little nipple-shaped termination to the cochlea has been broken off.

PLATE 20, FIG. 7.

The Right Membranous Labyrinth of the Penguin, *Spheniscus demersus.* × 5. The organ is viewed from the inner aspect and is rotated a little counter-clockwise. Numerous small air-bubbles are present in the vestibule and a portion of the canals. The cristæ acusticæ in the ampullæ are "simple." It will be noticed that the lagenar portion, *l.*, is relatively large. The perilymph recess is seen to the right of the cochlea, *c.*, and there is an oval opening, *d.p.*, on the upper posterior surface of the cavity. This opening corresponds with that found in the same position in the monitor and has not been found in any other bird hitherto examined. It is, however, represented in other birds by a short tube, the aqueduct of the perilymph, as described in the text.

s., superior canal.
p., posterior canal.
h., horizontal canal.
c.f., cartilaginous framework of cochlea.

PLATE 20, FIG. 8.

The Right Membranous Labyrinth of the Penguin, *Spheniscus demersus*. × 5. The organ is viewed from the outer aspect, above and in front. As the arch of the horizontal canal passes under that of the posterior canal at *x* it comes into contact with the latter, but there is no actual channel of communication between the two canals.

c., cochlea. *p.* posterior canal.

PLATE 20, FIG. 9.

Portion of the Right Membranous Labyrinth of the Penguin, *Spheniscus demersus*. × 10 *ca.* Viewed from behind and below. The lower part of the perilymph recess has been removed along with the round window (if present in this bird). The oval opening, *o.o.*, from the cochlea, *c.*, into the perilymph recess is clearly seen, and is bounded along one border by the lower limb of the cartilaginous framework, *c.f.*, in the cochlea. The bending of this cartilaginous framework is seen at the vestibular end of the cochlea. The tegmentum vasculosum, *t.v.*, has been to a considerable extent destroyed, but a fragment may be seen at the vestibular end of the cochlea. *l.*, lagena.

PLATE 20, FIG. 10.

The Right Membranous Labyrinth of the Spiny Ant-eater, *Echidna aculeata*. × 6. Viewed from the outer aspect and below. The semicircular canals are well curved and similar to those of other mammals, while differing from those of the platypus (see text). The perilymph space is fairly well marked in the canals and can be traced easily round the whole circumference. The cone-shaped recessus utriculi, *r.u.*, is seen lying between the ampulla of the horizontal canal, *h.*, and the outer wall of the utricle; and the nerves supplying the ampullæ and recessus utriculi are also seen. The oval window, *f.o.*, is almost circular in shape and looks directly into the saccule. Immediately to the left of the oval window the perilymph recess, *r.p.*, may be seen opening out of the cochlea as an egg-shaped cavity, and the round window, *f.r.*, is seen on its outer surface as an oval opening. At its posterior extremity the perilymph recess again narrows down and tapers off into the aqueduct of the perilymph. The latter channel only occupies a portion of the irregular mass at the lower left-hand corner of the plate, a portion of the jugular vein, *j.*, being also present in the mass. In this mass, however, the aqueduct of the perilymph, *p.a.*, is seen on the right side as a somewhat lighter band. The cochlea, *c.*, is well curved, and the lagena, *l.*, may be seen as a kidney-shaped structure at the tip of the cochlea on the side nearest to the vestibule. The irregular slit at the tip of the cochlea is an artefact produced by the long immersion of the head in alcohol. The white deposits in the different parts of the organ are not to be looked upon as otoliths unless their presence in these situations is confirmed by further examinations (see text).

s., superior canal. *h.*, horizontal canal.
p., posterior canal. *n.s.*, nerve to ampulla of superior canal.

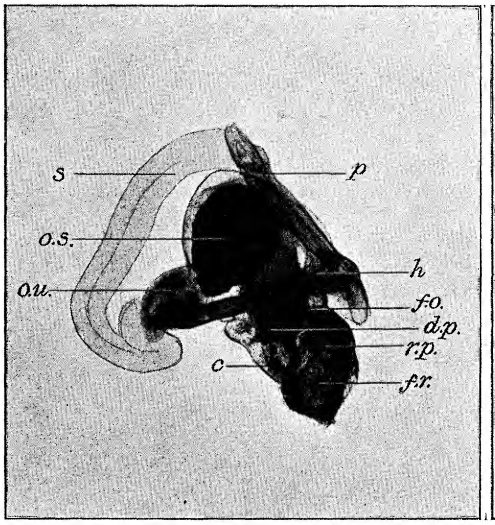


FIG. 1.

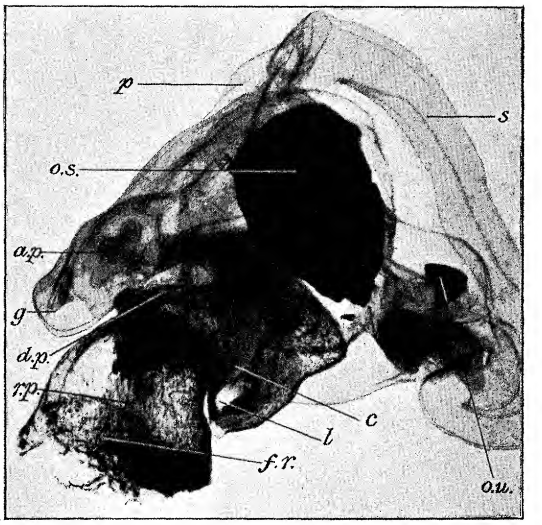
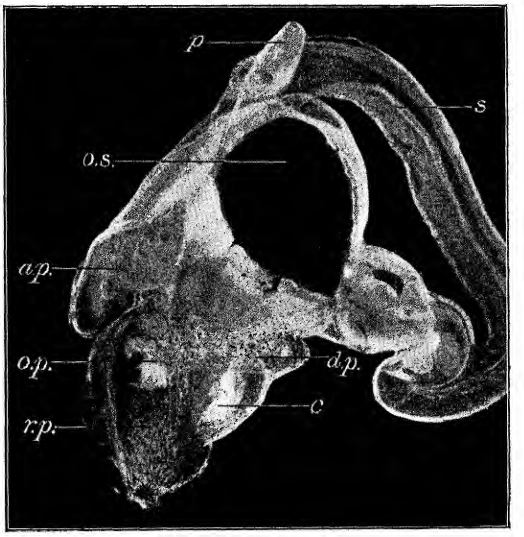
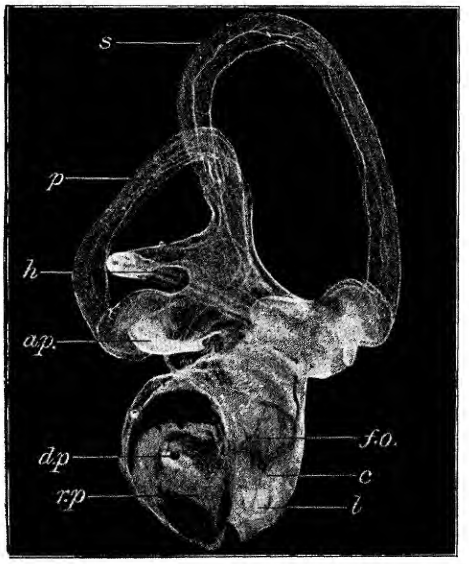


FIG. 2.

FIG. 3.





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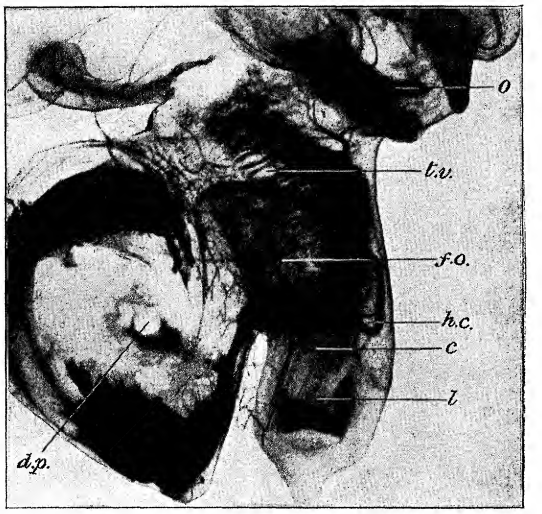

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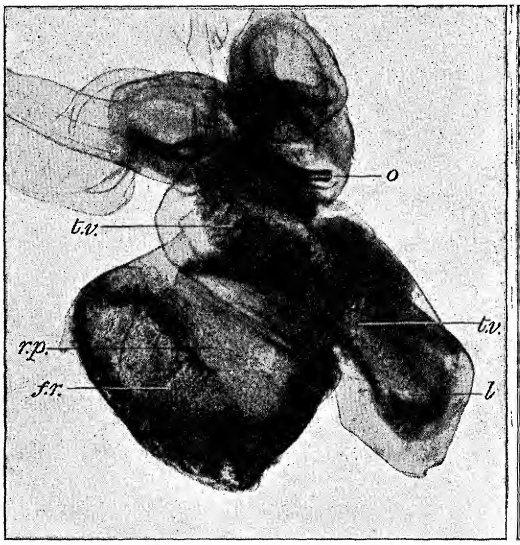

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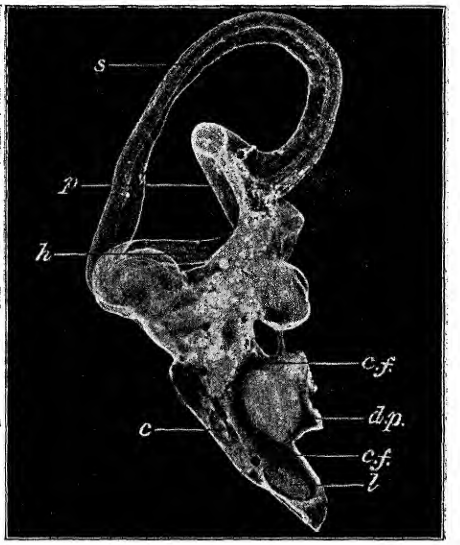
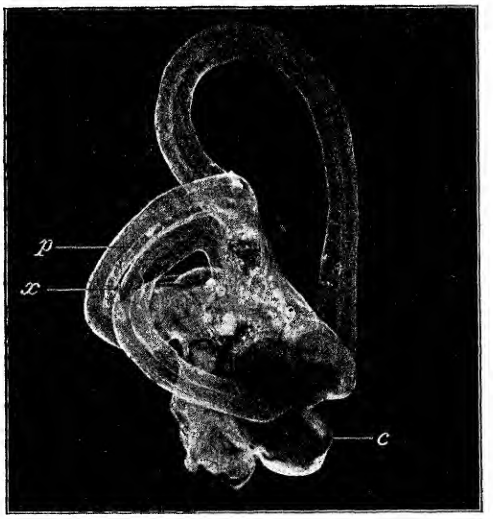


FIG. 7.

FIG. 8.



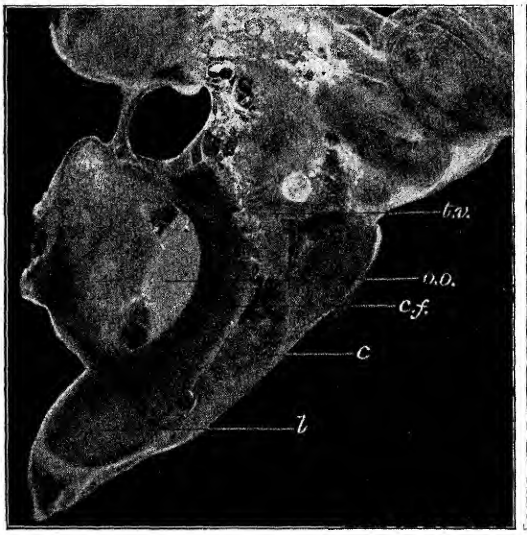


FIG. 9.

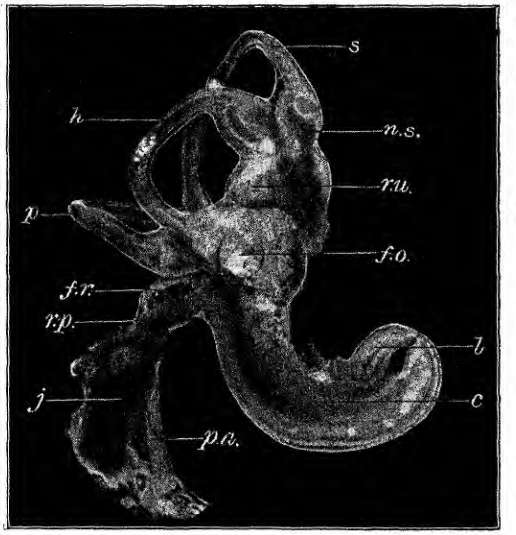


FIG. 10.

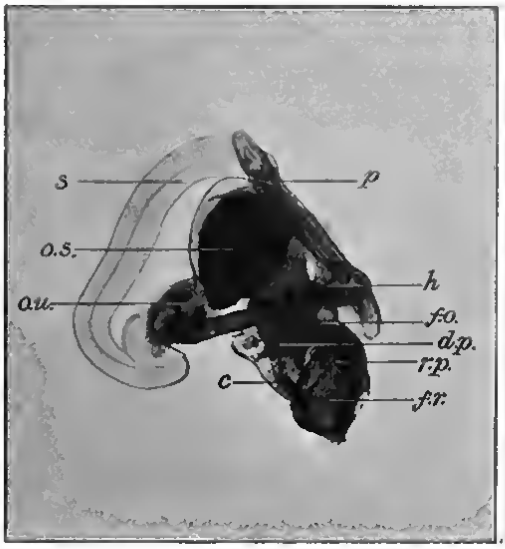


Fig. 1.

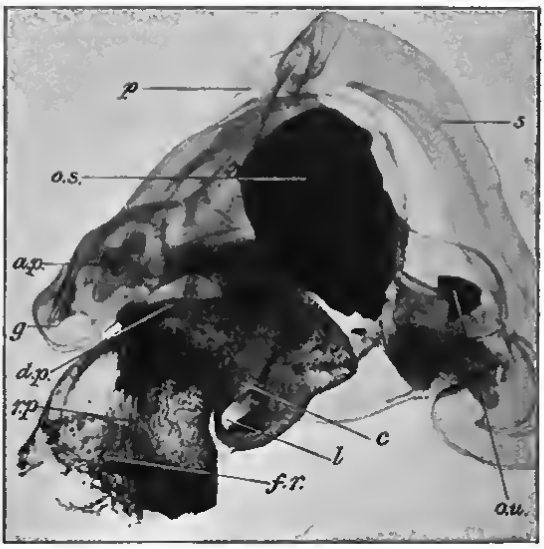


Fig. 2.

Fig. 3.

Fig. 4.

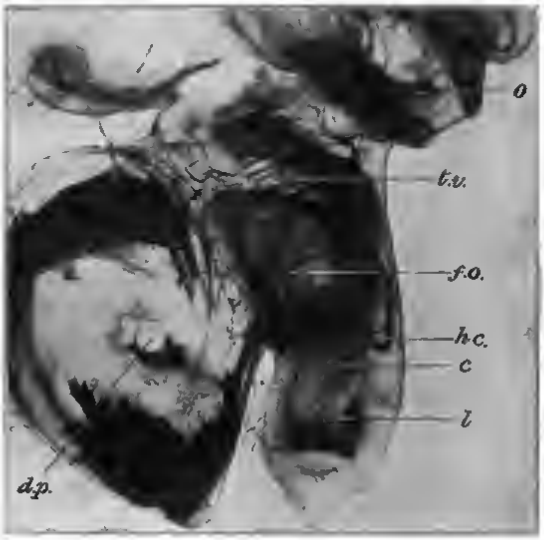


Fig. 5.

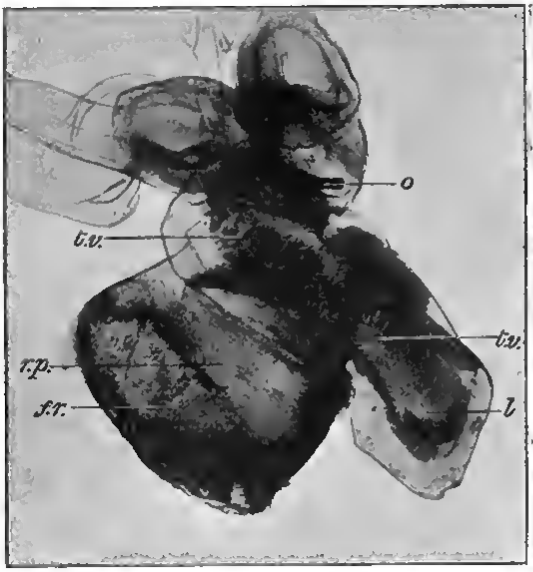


Fig. 6.

Fig. 7.

Fig. 8.

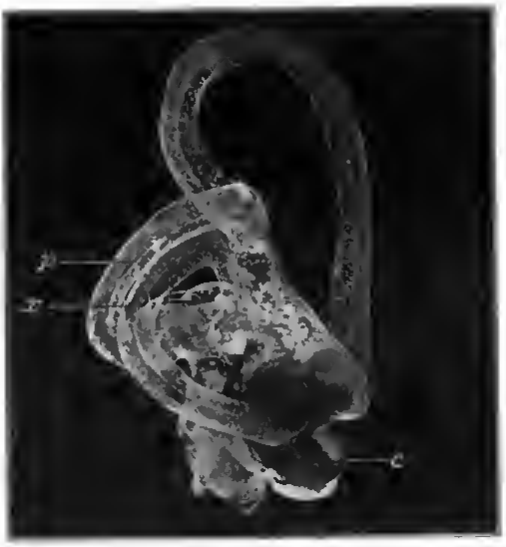


Fig. 9.

Fig. 10.